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The nature of the Old World savannah palaeobiome

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Writing in Nature Ecology & Evolution in 2018, we argued that there existed during the later Miocene of the Old World (ca 15-5 million years ago) "a single cohesive Old-World savannah palaeobiome of which the modern African savannah fauna is the surviving branch"[1]. Subsequently, Denk et al have taken issue with this interpretation and argued, using palaeobotanical data, that no such cohesive biome existed, and that a more compelling reconstruction sees mixed trees and shrublands dominant at that time[2]. In addition to defending our original interpretation we would like here to clarify some terms used in our paper, as we feel that much of the apparent discrepancy may actually reflect differences in terminology.

We used the term savannah in a broad sense, common in Neogene and Quaternary palaeoecology[3], meaning a woodland to grassland biome characterised by co-dominance of trees and grasses[4], the "mixed grass–tree biome" of Ref 5. In contrast, Denk et al, approaching the matter from a botanical perspective, adhere to a more restricted definition of savannah as grasslands. We formulated the term Old World Savannah Paleobiome (OWSP) to describe localities showing high similarity to our selected reference localities representing open-adapted large mammal communities: Lower Nawata, Pikermi, and Baode. These localities have all been previously identified as representing woodland-dominated, or mixed woodland-grassland ecosystems[6-9] through methods independent of mean ordinated hypsodonty. The evidence includes microwear, mesowear, stable isotope, phytolith, sedimentological, and functional morphological approaches, and covers Late Miocene sites from Turkey, Hungary, Bulgaria, Greece, Iran, and China[6-16]. Denk and colleagues' critique of our interpretations therefore stands against a wide, multiproxy literature repeatedly confirming the dominance of woodland and grassy woodland environments across a wide swath of Eurasia and Africa during the late Miocene.

We used the term cohesive, to which Denk et al[2] object, to imply interconnectedness of the faunal assemblages rather than uniformity of vegetation cover, which we should have made more explicit. The genus-level similarity analysis of large mammal faunas was used to trace the origin and dispersal of mammals within the OWSP as it expanded and contracted, in sync with the environment as approximated by mean hypsodonty (our figures 2 and 3)[1]. It was cohesive in the sense of connectedness of internal dispersal, not in the sense of being at all times and in all places a uniform system. We propose that in the OWSP, the diverse habitat of the Hipparion fauna[17], increasing overall and seasonal aridity created a world in which herbivores were progressively adapting to similar limiting conditions over vast areas.

It is not unexpected for phytological and zoological proxies to result in differing reconstructions. Even present-day mammal zoogeography (e.g., Ref. 18, Fig. 3c) does not exactly match

terrestrial vegetation biomes (e.g., Ref. 19, Fig. 4.3). Within a zoogeographic region, the terrestrial vegetation biomes may vary from semi-desert to forest. It has also been suggested that vertebrate fossils and macrofossils/palynomorph floras may reflect different environmental conditions and climatic cycles[9] though space prohibits further discussion here.

In principle, the existence of vegetational differentiation – including forests – within the large area covered by the OWSP is of course inevitable and we never doubted it. Indeed, such heterogeneity is also suggested by our own results, e.g., our Figs 2-3[1]. We deliberately used the robust but coarse metric of mean ordinated hypsodonty as a proxy for environmental harshness in general[20]. We did so because we expected that, while the local details would vary, the overall effect would be one of lowered ecosystem productivity, increased seasonality, and other factors contributing to harshness. Although more detailed ecometric models of climate or vegetation were available, we accordingly selected mean hypsodonty as the appropriate metric[21-25].

Denk and colleagues' paper[2] is a welcome opening towards the holistic survey of evidence and we look forward to discovering what exactly the floristic patterns mean in terms of habitats and ecosystems, and whether there is any actual disagreement in the reconstructions or interpretations of either of the methodologies.

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